# THE FOOD OF THE LARVAE OF *CHLOËON DIPTERUM* L. AND *BAËTIS RHODANI* (PICTET) (INSECTA, EPHEMEROPTERA)

By D. SEYMOUR BROWN

*Department of Zoology, University of Leicester**

## INTRODUCTION

In early accounts (Pictet 1843, Lampert 1899) the larvae of the Ephemeroptera were described as carnivorous on the basis of the strong development of their mouthparts. Wissmeyer (1926) reviewing previous work pointed out that the two commonly held views of the nature of the food, that it was purely animal or that it was mixed, were opposed to each other, and that both were contradicted by Sachse & Wohlegemuth (1916) who found only plant material in *Chloëon dipterum*. According to Wissmeyer (1926) *C. dipterum* captured and ingested live *Daphnia* and copepods in the laboratory, while in the field the food was almost entirely herbivorous. Algae and vascular plant tissue were the main food components in several North American genera (Morgan 1913, Traver 1925) including *Callibaëtis*, a genus which closely resembles *Chloëon* in its structure and mode of life. The results of more recent work support the conclusion that the food of the larvae of Ephemeroptera is very variable in composition. Badcock (1949) described only plant material from *Baëtis* sp., *Ecdyonurus torrentis* Kimmins and *Rhithrogena semicolorata* (Curtis), whereas detritus of unidentifiable origin was the main food component in *Baëtis rhodani*, *Siphlonurus lacustris* Eaton and *Rhithrogena semicolorata* (Jones 1950, 1958). Dunn (1954) included larvae of Ephemeroptera in both the detritus and plant feeding brackets of a 'food chain' for Bala Lake, Merioneth, while *Chloëon dipterum* and *Leptophlebia vespertina* (L.) were regarded as solely algal feeders in a Lancashire pond (Popham 1955). In artificial ponds the ephemeropteran larvae were found to subsist entirely on phytoplankton and epiphytic algae (Vaas & Vaas-van Oven 1959). *Stenonema pulchellum* was found to be exclusively herbivorous and was treated as a true primary consumer by Trama (1957), and other Heptageniids appear to be responsible for practically all the primary conversion of plant to animal matter in certain Colorado streams (Dr D. L. Abell, personal communication).

It follows from the variable nature of the diet that the larvae of Ephemeroptera do not all play the same part in the trophic structure of the communities in which they occur, and in view of this detailed knowledge of their feeding habits is highly desirable. To be complete such knowledge must include information on the variation that is likely in any particular species. Three possible sources of variation are seasonal changes in the environment, local differences between habitats, and differences between larvae of different sizes. These sources of variation were studied in larvae of *Chloëon dipterum* and *Baëtis rhodani* over a period of 18 months in south-east Leicestershire. Particular attention was paid to the feeding habits of the smallest larvae (0·5-1·0 mm) because as a result of the enormous numbers present (Macan 1957) it is probable that they play as great a part in the trophic structure of the community as at later stages in their growth.

* Present address: British Medical Research Council, c/o Department of Zoology, British Museum (Natural History), Cromwell Road, London S.W.7.

There is much fragmentary information on the food of the larvae of Ephemeroptera that is based on any or all of three considerations: the food as it appears to be available in the natural habitat; feeding behaviour in captivity; and analyses of gut contents. In studies of the last category conclusions are often drawn from a small number of observations and in relatively few cases has an attempt been made to assess the composition of the food accurately. Records of the composition of the food of single samples of larvae are given by Rawlinson (1939), Kolesov (1927), Badcock (1949), Jones (1951) and Dunn (1954). Several of these authors record the sizes of the larvae dealt with but the only comments on size differences in the food are by Ivanova (1958). A comparison of the food of a few samples taken over a period of 2 or 3 months is made by Wissmeyer (1926) and Jones (1950); Moon (1938) studied the food of *Leptophlebia* and *Caenis* over a period of 10 months. The only author to consider local differences in the food is Wissmeyer who examined *Chloëon dipterum* from two habitats. It is evident that the relative importance of the various food components varies greatly and that seasonal, local and size differences do occur. In order to define more clearly the extent of these differences it is necessary to use a method of analysis of the gut contents that allows sufficiently accurate examination of a large number of samples of larvae.

## METHODS OF FOOD ANALYSIS

The gut of an ephemeropteran larva usually contains a mixture of mineral particles, fragments of vascular plant tissue, various kinds of algae, and brown-coloured organic matter of unidentifiable origin which in the present study is termed *detritus*, a word that has been used in a wider sense by some authors to include higher plant tissue and mineral matter. A similar diet is found in plecopteran and trichopteran larvae, and the methods that have been used to investigate the gut contents of these groups of insect larvae are similar to those applied to freshwater fishes which are reviewed by Hynes (1950). Three basic methods may be defined, although two or three may be combined in the procedure of one worker.

### *Method of frequency of occurrence*

The number of animals in a sample in which each food component occurs is recorded, and usually expressed as a percentage of the total sample. This method was employed by Jones (1950), Badcock (1949), Slack (1936) and Ivanova (1958), and its simplicity allows the rapid treatment of large numbers of samples of larvae, although it can give no more than a preliminary picture of the diet because it fails to reveal differences in the relative proportions of the major food components in larvae taken at different times or places. This objection to its use is very important in the case of *Chloëon dipterum* and *Baëtis rhodani*. In these species the major food components, detritus and mineral particles, occur in almost all larvae, so that a series of 100% values would be obtained by the method of occurrence for these components, giving no indication of the big differences in their relative and absolute amounts in different samples.

### *Method of dominance*

The proportion of animals in a sample in which each food component is dominant on the basis of bulk, estimated by eye, is recorded. This method may be combined with the method of occurrence, and gives a more accurate picture of the composition of the food. However, in animals where the major food component is constant (in the case of *B. rhodani* this is detritus), the method provides no information about the abundance of lesser components or of the differences in the absolute bulk of the major component between different samples of animals.

### *Points method*

The food components are awarded a score on an arbitrary scale. The method was introduced by Wissmeyer (1926) who awarded the various algae in the gut contents points according to their abundance, and recorded detritus and mineral together as a percentage of the total volume of the food. This method suffers from the disadvantage of the lack of a quantitative basis. The score of points awarded to the algae was based on their abundance relative to each other, and hence only the qualitative composition of the algae in the food could be compared between different samples. Similarly, while the proportion of detritus and mineral present in the food of August and October larvae could be compared, there was no means of assessing the difference in the absolute amount of food consumed, because there was no accurate index of the total amount of food in the gut.

Hynes (1950) employed a more accurate points method in his investigation of the seasonal and local differences in the food of *Gasterosteus*. The components of the stomach contents were awarded points according to the proportion of the total volume of the contents that they occupied. Further, each stomach was awarded a score of points according to its degree of fullness, and this was divided proportionally among the scores of the components. The resulting total scores were an index of the abundance of the components that could be compared directly between different samples of animals of roughly the same size. A practical difficulty of this method as far as small insect larvae are concerned lies in the fact that in order to identify the food components it is necessary to examine the food under a monocular microscope, and the necessity of examining many fields of view makes it very difficult to assess the relative proportions of the materials present by eye.

### *Counting methods*

Under this heading may be considered the method devised by Hanna (1957) to produce results that could be subjected to statistical analysis. The gut contents of a number of larvae of approximately the same size were made into a fine suspension in 5 ml of water in a specimen tube which was shaken vigorously immediately before a subsample of 0·2 ml was removed by means of a micropipette. This was examined under a monocular microscope in a cell formed by a wooden ring cemented to a slide. Ten fields of view selected at random were examined with a squared eyepiece at a magnification of $\times 100$; the numbers of cells of the various diatoms and desmids, the length of pieces of filamentous algae, and the area of the grid occupied by pieces of vascular plant tissue, mineral and detritus were recorded. The total amounts of these food components present in the subsample were calculated, and the results were finally expressed as the total amounts occurring in a single larva. In calculating the standard error of the values obtained Hanna (1954) assumed that, shaking by hand produced a random distribution of the food particles within the suspension while a subsample was withdrawn, and that food particles were distributed randomly within the ring while fields of view were counted. He tested neither of these assumptions by the statistical analysis of a series of trial counts, and in view of the difficulty of judging by eye whether a distribution is random or not (Lund, Kipling & Le Cren 1958) it was thought necessary to do this before the method was adapted for use with *Chloëon dipterum* and *Baëtis rhodani*. The distribution of a particular species of diatom in suspensions of the gut contents of each of fourteen samples of large larvae of *B. rhodani* was tested by completely counting three subsamples withdrawn from each. A $\chi^2$ test was applied to each replicate group of three counts, and it was found that in no case was it very unlikely ($P<0{\cdot}01$) that the distribution of the diatom was random. The distribution of another diatom within subsamples that had been transferred to a ring on a microslide was tested by making five counts of thirty fields of view in different parts of the ring for each of thirteen subsamples. Before the counts were made the material within the ring was stirred until the distribution of the particles appeared to be random, but application of the $\chi^2$ test to the counts showed that in six cases it was very unlikely that this was so. The complete data of these tests, in which the conditions employed by Hanna were reproduced as far as possible, are available in an unpublished thesis (Brown 1959). In view of the results obtained, the calculation of numbers of algal cells and quantities of other food components from partial counts of subsamples on the basis of a random distribution of particles was considered not to be justified.

### *The method of food analysis used*

An important object in the investigation of the food of *Chloëon dipterum* and *Baëtis rhodani* was to estimate differences in the diet of the larvae at different times of the year and at different places, and a desirable feature of the method used to do this was that the likely error in the results should be known, so that the significance of the differences between them could be judged. If it were possible to separate the food components mechanically and weigh them this would be the ideal way of analysing the food of animals from a natural population, because absolute quantities would be obtained without the introduction of errors due to subsampling and counting. Such separation is practically impossible in the case of a small animal feeding upon a complex mixture of particles and various species of algae, and to obtain accurate results an optical counting method must be used in spite of its slowness.

The technique adopted here involved taking a subsample from a suspension of the food of a large number of larvae as was done by Hanna, and counting this completely in a sedimentation tube of the type described by Lund, Kipling & Le Cren (1958). In this way the source of error in Hanna's work was avoided and confidence limits could be calculated for the results on the reasonable assumption that they represented a random sample of the food. This is a desirable feature of all techniques by which numbers of organisms or particles are estimated, because where random distribution has been demonstrated, confidence limits for single counts can be read off rapidly from tables published by Pearson & Hartley (1954) or calculated by means of a simple formula (Ricker 1937). A rapid method of testing the significance of a difference between two such counts is given by Pearson & Hartley, but for most practical purposes it is adequate to apply the criterion that the difference between counts is significant if their confidence limits do not overlap.

Larvae of *Chloëon dipterum* and *Baëtis rhodani* were collected from three ponds and three streams respectively which are described later. Larvae of small, medium and large size were fixed immediately in the field in 5% formalin, and were sorted in the laboratory into the size-groups 0-1 mm, 4-5 mm and 6-7 mm. As many larvae of a particular size as were available within a convenient collecting time were taken, with a maximum of forty to fifty for each size-group. Collections were made at approximately fortnightly intervals from January 1958 until June 1959, and in none of the habitats was any decrease in the population apparent. The contents of the anterior part of the gut, extending to the base of the second abdominal segment, were separated with fine needles in a drop of 5% formalin. The procedure was repeated until a suspension had been made of the food of all the larvae available for a particular size-group, date and locality. This was transferred to a specimen tube (3 × 1 in.).

In the case of the 4 and 6 mm larvae the volume of the suspension was made up to 15 ml, and a subsample of 0·25 ml was withdrawn by means of a micropipette inserted in the cork, immediately after the tube had been shaken vigorously for 5 sec. This was transferred to a sedimentation tube consisting of a short length of glass tubing of 12 mm diameter cemented to a microslide by means of waterproof adhesive 'Araldite'. The sedimentation tube was placed on the stage of an inverted microscope fitted with a squared eyepiece grid and allowed to stand for 1 h, during which time the suspended particles settled to the bottom of the tube. By systematic movements of the mechanical stage the whole of the floor of the sedimentation tube was scanned, no area being covered twice. The numbers of diatoms and of pieces of filamentous algae together with the number of cells present in each fragment were recorded. The number of squares of the grid occupied by detritus, particles of mineral, and vascular plant tissue was estimated to an accuracy of one-quarter of a square. In the case of the smallest larvae the whole of the food suspension was transferred to the sedimentation tube and counted as described above.

The way in which confidence limits were obtained for the estimations of the numbers of unicellular algae in the food has already been described. As far as the other important food components were concerned the calculation of confidence limits was more difficult. It was not attempted for colonial forms or for fragments of filamentous algae because for this purpose an estimation of the mean number of cells present in the colonies or pieces is necessary and the wide variation of cell numbers in the food of *Chloëon dipterum* (*Dinobryon* 1-12, *Spirogyra* 1-12, *Ulothrix* 1-20) resulted in confidence limits that were too wide to be of practical value. The distribution of particles of detritus within suspensions of the food of *Baëtis rhodani* was tested by counting the total area of the grid occupied in each of five subsamples of ten suspensions. The results of a $\chi^2$ test on these values did not justify the calculation of confidence limits for single counts on the basis of random distribution. However, in nine out of the ten groups of counts all the values lay within 40% of the mean. On this basis confidence limits of 50% were used for all the values obtained for detritus.

The values obtained for each food component by the counting of subsamples were multiplied by 60 so that values were obtained for the whole samples of suspension and were finally expressed for single larvae. The results obtained for 4 and 6 mm larvae are presented in Figs. 1 and 2.

There are certain aspects of the collection of samples of larvae for food analysis that must be considered when a comparative study of feeding is being made. A difficulty of all work in which animals are being studied in relation to their environment is the problem of precisely defining the environment. In the case of freely mobile larvae such as *Chloëon dipterum* and *Baëtis rhodani* the difficulty is acute because while their habitats may be described respectively as pond and stream, a host of microhabitats, many of them capable of further subdivision, may be defined within these habitats. It is possible that no two loci, even though they lay adjacent on the bed of the pond or stream, would provide exactly the same feeding conditions to a larva. In practice, where the food of a population is being studied in relation to changes in the environment, the composition should be assessed from as large samples of larvae as possible from a large uniform area of habitat. In order to achieve this as nearly as possible the samples of *Chloëon dipterum* and *Baëtis rhodani* were collected in each locality from the same area of homogeneous habitat over which the feeding conditions appeared to be uniform.

In addition to changes in activity that may occur in response to light and temperature, many insects show a daily rhythm of activity that is independent of obvious external factors (Harker 1958). The larvae of *Ecdyonurus torrentis*, *Baëtis rhodani* and *Heptagenia lateralis*, showed an activity rhythm with peaks every 3-4 hours (Harker 1953b). It would appear to be likely that the intensity of feeding is affected by such rhythms, and in view of this it is desirable that samples of larvae should be collected at the same stage in the feeding cycle when the food of different samples is to be compared. An attempt to do this was made by collecting the samples of *Chloëon dipterum* and *Baëtis rhodani* during a period of 2 hours in the middle of the day.

Both Jones (1950) and Badcock (1949) comment on the readily observable fact that freshly moulted ephemeropteran larvae contain no food in the gut, which is also the case in those that are about to moult. Fríden (1958) demonstrated a regular fluctuation in the intensity of feeding between successive ecdyses, which followed a specific pattern, in many species of larval Lepidoptera. It is probable that a fluctuation in feeding activity related to the hormonal changes associated with moulting is a phenomenon occurring in many insects, so that where a comparative study of feeding is being made it is desirable that the samples should be composed of larvae in the same physiological state. When natural populations are being investigated this is very difficult to achieve, but this source of error was minimized by excluding from the samples of *Chloëon dipterum* and *Baëtis rhodani* freshly moulted larvae and those that were nearing emergence.

## HABITATS

Larvae of *Chloëon dipterum* were collected from three ponds: Whites Barn — nat. grid ref. 43/708074; Baggrave — 43/696086; Quenby Willows — 43/709052. Larvae of *Baëtis rhodani* were collected from three streams: Fludes Lane — nat. grid ref. 43/635003; Stoughton — 43/636018; Red Lodge — 43/755075. The habitats contained large populations of larvae and were chosen because of the different feeding conditions that they appeared to present. Collections were made from January 1958 to June 1959. The life cycle of *Chloëon dipterum* is univoltine while that of *Baëtis rhodani* includes two main generations each year (Macan 1957). The effect of this difference on the availability of the sizes of larvae required for food analysis was most marked in the case of the 0-1 mm group. Larvae of *Chloëon dipterum* of this length were present from July until September 1958 in all three ponds, whereas *Baëtis rhodani* of this size were collected in most months of the sampling period, being particularly abundant in the winter months and in June and July. Larger larvae of both species were absent or scarce on several occasions in late summer but were abundant in the majority of collections taken.

Each time that a collection was made, observations on the habitat were recorded in the form of remarks on the abundance of algae, the amount of detritus, the condition of the aquatic vascular plants, and the abundance of plant material of allochthonous origin. These observations were supplemented by the examination in the laboratory of samples of detritus, vegetation and scrapings from stones. The observations are included in the descriptions of the habitats given below. The German word 'aufwuchs' is used as a convenient term for the growth of algae, together with the detritus that it usually contains, which coats subaquatic surfaces.

*Whites Barn*

Surface area 150 sq. yd, depth 4-6 ft; maximum temperature recorded 21·0° C.

There was no cover on the steep banks of this pond apart from meadow grasses which for most of the year extended below the water surface and among which large numbers of *Chloëon dipterum* were present. The sampling station was at the pond edge among grasses, *Juncus*, and *Potamogeton natans*. The latter was the dominant aquatic vascular plant, large areas of the bottom being covered by *Nitella* (Characaee).

In contrast to the other habitats the material collected in the plankton net was always greenish and very rich in algae, and a thick aufwuchs was usually visible on the submerged vegetation. A heavy growth of aufwuchs was present in February 1958, but this decreased so that by the middle of April very little was visible. A big increase occurred in the middle of July that was followed by a slight decrease in October. In early 1959 no decrease in the amount of aufwuchs was observed and it is probable that this was related to the higher temperatures that occurred at this time in comparison to 1958.

The bulk of the material collected in the plankton net consisted of filamentous algae, and detritus that was often aggregated together by brown ramifying fungal hyphae. Small *Chlorophyceae*, particularly *Tribonema* and *Ulothrix* were abundant throughout the year. *Spirogyra*, *Oscillatoria* and filamentous *Fragilaria* were usually present. A stout form of *Closterium* resembling *C. leibleinii* was most abundant during the summer months while an elongate slender form resembling *C. aciculare* was very abundant in the winter. Of the solitary diatoms, *Rhopaloidia* and a large *Navicula* were the most abundant, the latter being mainly a winter species. Species of *Synedra*, *Nitzschia* and *Cocconeis* were fairly abundant in spring, and occasional specimens of *Gyrosigma* and *Cymbella* were noted.

Whites Barn pond received no inflowing stream or drainage channel and the inflow of allochthonous material seemed to be slight. As the nearest tree was situated 30 yd away, very few dead leaves appeared in the water in the autumn. The detritus in this pond was thus of autochthonous origin although the presence of small quantities of mineral particles in the food indicated that a small amount of material was washed in from the banks.

*Baggrave*

Surface area 120 sq. yd; depth 1-4 ft; maximum temperature recorded 14·0° C.

This was an artificial pond formed by the damming of a small stream, shaded at one end by a thicket of oak, ash and hawthorn trees. The macroflora consisted entirely of *Ceratophyllum demersum* in which *C. dipterum* was very abundant.

*Ceratophyllum* was abundant throughout the sampling period, reaching a maximum in July, when it rapidly died off so that the sampling station was choked with dead fragments among which larvae continued to occur in spite of the stagnation of the water from which a sulphurous smell arose.

The seasonal fluctuation in the abundance of the algae closely followed that at Whites Barn although algae never clogged the plankton net as at Whites Barn. From April to October 1958 no filamentous algae were observed in the habitat, and the *Ceratophyllum* had a very clean appearance, being almost free from aufwuchs. From October 1958 to February 1959 an increase took place and filamentous algae were more abundant than ever before. No decrease had taken place by June 1959 when sampling ceased.

In the spring of 1958 the common filamentous algae were *Ulothrix* (together with *Tribonema*), *Oedogonium* and *Fragilaria*. A blue green alga resembling *Oscillatoria* was common in September and October. In February 1959 thick tufts of *Mougeotia* appeared and this alga continued to be abundant, with a little *Spirogyra* until June. *Fragilaria* was abundant from February until May and was more common than at Whites Barn. The non-filamentous algal flora at Baggrave differed in composition as well as in absolute abundance from that at Whites Barn. Relatively more common were *Cocconeis*, and large species of *Nitzschia* and *Synedra*. *Navicula*, *Closterium leibleinii* and *C. aciculare* were relatively much less common than at Whites Barn, while *Rhopaloidia*, *Gyrosigma*, *Asterionella*, *Dinobyron* and *Peridinium* were not recorded at all. The diatom species were all much more abundant in the winter and spring than in the summer.

In contrast to Whites Barn, Baggrave received an inflowing stream and the proportion of detritus in the aufwuchs on the *Ceratophyllum* varied according to the quantity of allochthonous material that was deposited in the pond. In both years a peak was reached in early spring after the melting of the ice. In autumn a big influx of allochthonous material was provided by the leaves of the ash and oak trees that overhung the pond.

### *Quenby Willows*

Surface area 400 sq. yd; depth 1-4 ft; maximum temperature recorded 15.5° C.

Larvae were collected from among the roots of a large willow tree where, duıing the early part of the year, a growth of *Callitriche* developed which began to rot in May and had disappeared by the end of June. Very little alga was visible during the sampling period. A filamentous blue-green species resembling *Oscillatoria* and a gelatinous colonial form resembling *Nostoc* were present among dead willow leaves from May to July 1958. Small amounts of *Fragilaria* were also present in May 1958.

Non-filamentous algae were less abundant than at either Whites Barn or Baggrave, but showed the same seasonal fluctuations in abundance. Most of the forms found in the other two ponds were present. *Gomphonema* was particularly abundant in the spring of 1958, and *Closterium leibleinii* in the spring of 1959. *Rhopaloidia*, *Closterium aciculare*, *Dinobryon* and *Peridinium* were not recorded.

Detritus showed no variation in composition or abundance throughout the sampling period and was composed mainly of faecal pellets of *Asellus meridianus* that were feeding upon the dead willow leaves in large numbers.

### *Fludes Lane Stream*

Maximum temperature recorded 15·0° C.

*Baëtis rhodani* was collected from this stream where it flowed through a small wood. The width varied from 4-6 ft and the bottom was stony. There was a poor growth of algae until March 1959 when probably as a result of the increased illumination of the stream due to clearing of the wood a very big increase took place and the stones became covered with a thick slime of epilithic organisms. Until this time *B. rhodani* had occurred in profusion but after the end of March none were found in several collections made at the usual collecting station and in other parts of the stream. At all places the stones were thickly coated with slime and the disappearance of *B. rhodani* appeared to be related to this. It may be that the disappearance of the larvae and the appearance of the rich algal slime were independent results of organic pollution or that the larvae were unable to feed upon the slime which besides coating the stones covered the intervening areas of substratum. The latter explanation is supported by the continued occurrence of other organisms, including *Gasterosteus*, *Gammarus* and *Habrophlebia fusca* (Curtis), after *Baëtis rhodani* had disappeared.

Small amounts of *Chaetophora* were present in most of the samples of scrapings taken from stones. *Oscillatoria* and *Ulothrix* were spring and summer species respectively. Diatoms declined in abundance from January to August 1958. *Navicula curvata* and *Achnanthes minutissima* were the dominant species, while *Roicosphenia curvata*, *Cocconeis placentula* and *Gyrosigma* were usually present. There was a slight increase in numbers in the autumn. From the end of March 1959 a big increase occurred and at the end of April *Navicula curvata*, *Nitzschia lacunarum*, *Cocconeis placentula* and *Meridion circulare* were all very abundant and continued to be so until June when sampling ceased.

In autumn the stream bed was thickly covered with leaves from the overhanging ash trees. The amount of detritus coating the stones and lying between them was greatest after heavy rainfall when the water level rose from 4 in. to about 3 ft.

### *Stoughton Stream*

Maximum temperature recorded 13° C.

This was a narrow deeply cut stream, from 2-3 ft wide, flowing through pasture land. Fences prevented cattle from grazing the banks on which *Epilobium* and *Scrophularia aquatica* grew thickly in the summer. The shade of the vegetation on the banks kept the water comparatively cool, and, when the flow ceased entirely in May 1958 and June 1959, prevented isolated pools from drying up. It was surprising to find *Baëtis rhodani* in this habitat not only because the condition of the stream in summer was apparently so unfavourable to the species but also because of the nature of the substratum. In many places this was loose sand and unless the flow was very slack larvae were only able to maintain themselves on the clay bank or by clinging to grasses hanging in the water. In other parts small pebbles were present that were almost free from algae. In winter the depth rose to over 4 ft and the rate of flow was so rapid that hollows were gouged in the bottom and the pebbled stretches were covered with sand. In this unpromising habitat *B. rhodani* was common but not so abundant as in the other two streams. *Habrophlebia fusca* and *Centroptilum luteolum* (Müller) were also taken occasionally.

In comparison with Fludes Lane or Red Lodge there were very few algae of any sort in Stoughton stream. Small amounts of *Chaetophora* were sometimes present in samples of scrapings taken from stones. Diatoms were most abundant in the summer and *Navicula curvata* was usually dominant. A small *Nitzschia*, probably *N. palea*, was relatively common in May 1958 and in August and September a large species, *N. lacunarum*, was common. *Cocconeis placentula*, *Meridion circulare*, *Gyrosigma* and small species of *Achnanthes* and *Navicula* were also present.

The amount of detritus lying on the bottom of Stoughton stream was usually small as a result of the scouring action of the current.

### *Red Lodge stream*

Maximum temperature recorded 17° C.

In its width of 4-6 ft and its stony substratum this stream resembled Fludes Lane but contrasted with it in the thick growth of filamentous algae that was present on the stones throughout the sampling period. This difference was probably due to the absence of any shading of the water by trees at Red Lodge.

*Baëtis rhodani* was collected from among stones from which grew long tufts of a large species of *Chaetophora* that were overgrown by *Vaucheria* in the early spring. *Oscillatoria* and *Diatoma* were abundant for short periods in the summer. *Navicula curvata, Achnanthes minutisimma, Cocconeis placentula* and *Roicosphenia curvata* were the dominant diatoms, the last two being epiphytic on the *Chaetophora*. Numbers increased steadily from January to June 1958, a big increase in *Navicula curvata* in April being followed by an abrupt increase of *Roicosphenia curvata* and *Cocconeis placentula* in June. In July and August the numbers of all diatoms except *C. placentula* were small. A slight increase in October was maintained until February 1959 when numbers rose to a high level that had not fallen off by June. As in 1958 the increase of *Roicosphenia* took place after that of *Navicula curvata*. *Nitzschia lacunarum, Achnanthes* and *Fragilaria* were present in most of the samples. *Meridion circulare* appeared in March and April of both years and *Closterium* spp. were occasionally present.

The amount of detritus deposited on the stones and on the filamentous algae varied according to the amount of rainfall. Deposits were heaviest in the autumn and spring after periods of flooding. During July and August the *Chaetophora* was clean and bright green.

## RESULTS

Tables containing the complete results of the food analyses are available in an unpublished thesis (Brown 1959). The results are summarized below and those obtained for 4 and 6 mm larvae are depicted in Figs. 1 and 2.

### *The food of* Chloëon dipterum

A marked seasonal variation in the amount of food present in the gut may be attributed to variation in two factors: the amount of food available in the habitat, and the intenstiy of the feeding activity. The quantity of detritus ingested (Figs. 1 *a, d*) appeared to depend mainly on the second factor. In Table 1 the mean values for detritus recorded in 4 and 6 mm larvae over the periods January-March and May-July are compared. In autumn and winter generally low values were obtained in larvae from all the ponds in spite of the abundance of detritus at this time, and an obvious increase in the amount of detritus in Baggrave pond was not reflected in the food. In the summer no changes were observed in the habitats that could directly account for the rapid increase in the amount of detritus in the gut. Temperature rose in correlation with this increase and it appears that low temperature was the most important factor limiting the amount of food ingested by the larvae in winter, spring and early summer. Some evidence that the quantity of detritus ingested was also related to the quantity that was present in the habitat was found by comparing the fluctuation of detritus in larvae from Baggrave and Whites Barn. In 1958 and 1959 peak amounts of detritus were recorded from Whites Barn larvae 1-2 months earlier than at Baggrave. The fact that this was the case in both 4 and 6 mm larvae suggests that a local pattern of fluctuation occurred that, as temperatures were approximately the same in both ponds, was dependent upon local differences in the quantities of food available to the larvae.

In several samples of larvae collected after the middle of July and before the end of

September the amounts of detritus were small compared with those recorded in larvae collected earlier in the summer. No decline in temperature or decrease in the amount of food available in the ponds was observed that could have accounted for this, and it is suggested that these low values were due to a reduction of feeding activity due to a lowering of the oxygen concentration in the water.

Detritus occupied by far the largest part of the total volume of the gut contents in almost every sample. In composition it appeared to be the same in large and small larvae from the same pond, but in larvae from different ponds differences were observed; *e.g.* the detritus, both in the habitat and in the food, was darker in larvae from Quenby Willows than in those from other ponds, as a result of the high proportion of material derived from rotting willow leaves that it contained. A high proportion of this detritus had probably passed through the alimentary canal of *Asellus meridianus*, which was extremely abundant in the habitat.

Filamentous algae present in the food were predominantly small Chlorophyceae of which *Ulothrix* and *Tribonema* were identified. A few larger forms were occasionally present but these always lacked cell contents and were unidentifiable; it is probable that these cells were dead when ingested. Large filamentous Chlorophyceae that occurred abundantly in the habitats were not found in the food; neither were Cyanophyceae.

Table 1. *The spring and summer quantities of detritus (mean values in arbitrary units) in the food of larvae of* Chloëon dipterum *(% change in parentheses)*

| | Jan.-March | | May-July | |
|---|---|---|---|---|
| | 6 mm larvae | 4 mm larvae | 6 mm larvae | 4 mm larvae |
| Whites Barn | 9·3 | 4·9 | 56·0 (502) | 22·5 (359) |
| Baggrave | 17·6 | 9·2 | 29·5 ( 61) | 15·7 ( 70) |
| Quenby Willows | 25·6 | 4·2 | 40·8 ( 59) | 14·2 (245) |
| Mean (all ponds) | 17·5 | 6·1 | 42·1 (207) | 17·2 (221) |

Apart from the winter and early spring, when quantities present were large in the habitats and low in the guts, the abundance of filamentous algae in the food was correlated with that in the habitat. Greatest amounts were present from April to June in both years in both 4 and 6 mm larvae (Figs. 1 *b, e*). Larger amounts were recorded in 1959 than in 1958 at Whites Barn and Baggrave, in correlation with the higher temperatures and the greater abundance of algae in the habitats in 1959. Filamentous algae were generally more abundant in larvae from Whites Barn than elsewhere, and occurred in every sample of 4 and 6 mm larvae. Hardly any were recorded in larvae from Quenby Willows and none in many samples from Baggrave of both size-groups in the winter. None was present in the food of 0-1 mm larvae.

Non-filamentous algae contributed a very small proportion of the total volume of the food. Besides diatoms and desmids; unicellular Chlorococcales (referred to as coccoid cells), *Dinobryon* (Chrysophyceae) and *Peridinium* (Dinophyceae) were frequently present. Evidence of selective feeding by 4 and 6 mm larvae was obtained from Whites Barn where the algal flora was more varied than elsewhere. In comparison with small species, large species of algae of similar abundance in the habitat appeared relatively rarely in the food. That this selective feeding was due to the size of the algae is indicated by the fact that large algae occurred far less frequently in the 4 mm larvae when these were collected together with 6 mm larvae on the same date (Table 2). The algae found in the food of 0-1 mm larvae consisted mainly of coccoid cells and small *Cocconeis* with occasional specimens of *Achnanthes* and *Navicula.* Changes in the number and species of non-filamentous algae in the food resulted from variation in the feeding activity of the larvae and variation in both the abundance and specific composition of the algal flora in the habitats. High values were recorded in the spring of both years that were correlated with an increase in feeding activity and the presence of large numbers of algae (Figs. 1 *c, f*). Higher values were recorded at Baggrave and Whites Barn in 1959 than in 1958 as was the case for filamentous algae. The spring peaks were followed by a decline that was correlated with a decrease in the amount of algae in the habitats. Larvae from the three habitats showed differences in the amounts and species of filamentous algae that occurred in the food which were correlated with differences between the flora of the habitats. There were far fewer algae in the food of 6 mm larvae from Quenby Willows than from elsewhere in the spring of 1959, while of the 4 mm larvae those from Baggrave usually contained more than those from the other habitats.

Table 2. *Frequency of occurrence of large species of algae in 4 and 6 mm larvae of* Chloëon dipterum *collected on the same dates from Whites Barn pond (12 collections)*

| | 6 mm larvae | 4 mm larvae |
|---|---|---|
| *Closterium leibleinii* | 2 | 0 |
| *C. aciculare* | 5 | 2 |
| *Cosmarium* | 8 | 6 |
| *Navicula* | 12 | 1 |
| *Rhopaloidia* | 4 | 0 |
| *Gyrosigma* | 3 | 0 |

No seasonal pattern was observed in the occurrence of mineral particles and vascular plant tissue in the food. These food components were recorded most frequently and in largest amounts in larvae from Baggrave and Quenby Willows in correlation with the greater amounts of allochthonous material that was deposited in these ponds by inflowing streams and overhanging vegetation. Occasionally vascular plant tissue occupied as great a proportion of the total volume of the food of 6 mm larvae as detritus. Vascular plant tissue occurred more frequently in the food of 6 mm larvae than in 4 mm larvae (Table 3). Neither mineral particles or vascular plant tissue were found in the food of 0-1 mm. larvae.

Table 3. *Frequency of occurrence of vascular plant tissue* (vp) *and filamentous algae* (fa) *in the food of 4 and 6 mm larvae when these were collected on the same date*

| | Food material | Number of collections | 6 mm larvae | 4 mm larvae |
|---|---|---|---|---|
| *Chloëon dipterum* | | | | |
| Baggrave | vp | 13 | 4 | 1 |
| Quenby Willows | vp | 11 | 7 | 3 |
| *Baëtis rhodani* | | | | |
| Stoughton | vp | 13 | 8 | 4 |
| Fludes Lane | fa | 16 | 13 | 8 |
| Stoughton | fa | 13 | 3 | 2 |
| Red Lodge | fa | 17 | 13 | 7 |

## *The food of* Baëtis rhodani

As in *Chloëon dipterum* the food of all larvae consisted mainly of detritus, but in *Baëtis rhodani* the quantities present did not show a marked seasonal fluctuation that could be correlated with temperature. Thus, although lowest values were recorded in January and February when temperatures were low (Figs. 2 *a*, *e*) other values recorded at the same temperature were greater than many recorded in the summer. Similarly, largest quantities of detritus were present in the food in the summer when temperatures were high, but marked decreases occurred on several occasions when no corresponding decline in temperature took place. There was very little difference in the amounts ingested in the spring and summer months (Table 4) compared with *Chloëon dipterum* (Table 1).

The most important factor governing the frequent fluctuations in the amount of

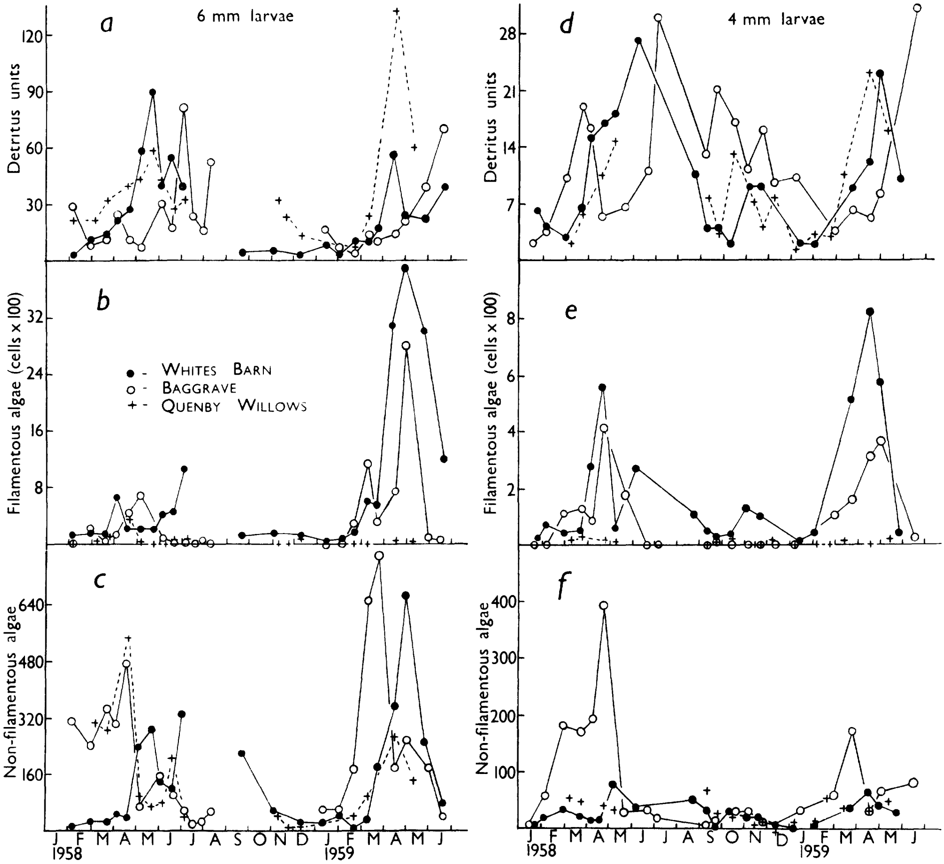


FIG. 1. Seasonal fluctuations in the food of *Chloëon dipterum: a-c*, 6 mm larvae; *d-f*, 4 mm larvae. The units used for detritus and mineral particles are the number of squares of the county grid occupied by these materials; for filamentous and other algae, the figures show the numbers of cells present.

detritus ingested by *Baëtis rhodani* appeared to be fluctuation in the quantity available to the larvae as food. Such fluctuations were not synchronous in the streams because they were often produced by local changes, such as disturbance by cattle and the digging of field drains. In addition, flooding, with the disturbance of detritus that it brought about, did not occur at the same time in all the streams. The generally lower values recorded in 1959 compared with 1958 showed that a variation in feeding conditions from year to year was reflected in the food ingested by the larvae. The frequent lack of correlation between the fluctuations occurring in 4 and 6 mm larvae from the same stream is difficult to explain, but may indicate a difference in feeding habits due to the occupation of different niches in the stream by larvae of these size-groups.

The few pieces of filamentous alga that occurred in the food always lacked cell contents

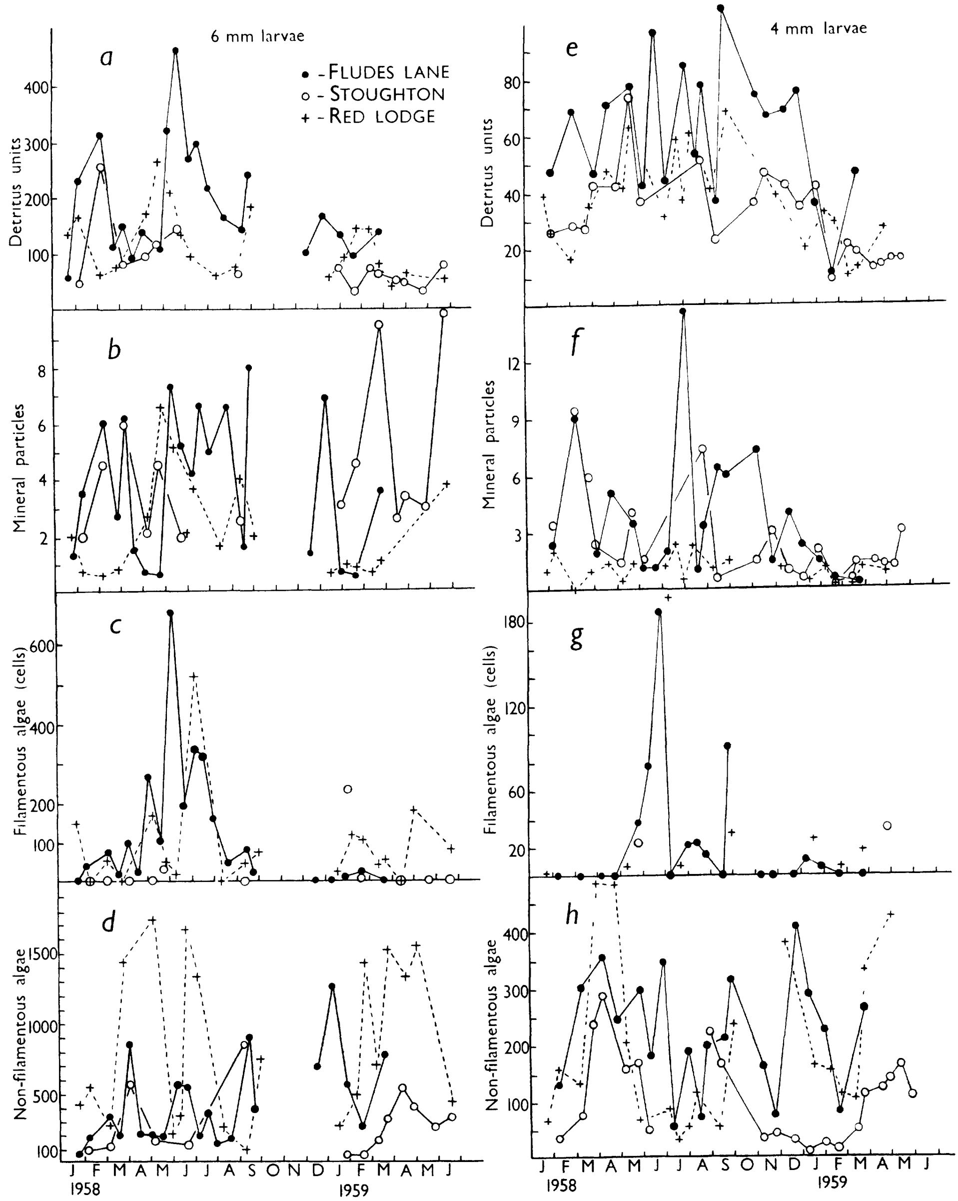


FIG. 2. Seasonal fluctuations in the food of *Baëtis rhodani*; *a-d*, 6 mm larvae; *e-h*, 4 mm larvae. For the units used see legend to Fig. 1.

and consisted mainly of the tips of filaments of *Chaetophora*. Largest amounts were present in the food in the summer (Figs. 2 *c*, *g*) when algae were most abundant in the streams. Filamentous algae occurred in very small amounts in larvae from Stoughton and were often absent from the food altogether. It occurred in a smaller number of 4 mm than of 6 mm larvae when these were collected on the same date (Table 3). No filamentous algae was found in the food of 0-1 mm larvae.

Diatoms formed a very small proportion of the total volume of the food. Most abundant were *Navicula curvata*, *Roicosphenia curvata*, *Achnanthes minutissima*, *Cocconeis placentula* and *Gomphonema* sp. Wide fluctuations took place over short periods in the numbers present in the food (Figs. 2 *d*, *h*) which were correlated with fluctuations in the numbers in the habitats. Such a relationship was particularly clear in the case of 6 mm larvae from Red Lodge, in which successive peaks in the abundance of *Navicula curvata* and *Roicosphenia curvata* in the early part of 1958 were clearly reflected in the food. Local differences in the quantities and species of diatoms occurring in the food were related to the abundance and composition of the diatom flora in the habitats. Greatest numbers were present in larvae from Red Lodge and the smallest in larvae from Stoughton. Evidence of selective feeding was found at Red Lodge where *Roicosphenia* and *Gyrosigma* occurred in the 4 mm larvae relatively less frequently than in 6 mm larvae. In 0-1 mm larvae, *Achnanthes minutissima*, coccoid cells, and small specimens of *Cocconeis* were usually present, together with occasional small specimens of *Navicula curvata* and *Roicosphenia curvata*.

Table 4. *The spring and summer quantities of detritus (mean values in arbitrary units) in the food of larvae of* Baëtis rhodani *(% change in parentheses)*

| | Jan.-March | | May-July | |
|---|---|---|---|---|
| | 6 mm larvae | 4 mm larvae | 6 mm larvae | 4 mm larvae |
| Fludes Lane | 179·1 | 57·7 | 257·6 (+43) | 69·0 (+22) |
| Stoughton | 150·5 | 27·7 | 119·7 (−20) | 53·3 (+92) |
| Red Lodge | 108·5 | 29·4 | 177·1 (+63) | 46·1 (+56) |
| Mean (all streams) | 146·0 | 38·2 | 184·8 (+28) | 56·4 (+56) |

Vascular plant tissue was absent from the food of larvae collected at Fludes Lane, and occurred in only a few samples from Red Lodge. In larvae from Stoughton it was present more frequently in correlation with the large amounts of allochthonous vegetable material that this stream received. As was the case in larvae of *Chloëon dipterum* it occurred in the food of 4 mm larvae less frequently than in 6 mm larvae (Table 3). None was found in the food of 0-1 mm larvae.

Mineral particles were a constant component of the food of larvae of all sizes, and usually occupied the largest part of the total volume of the food after detritus. Amounts present varied widely and independently of detritus (Figs. 2 *b*, *f*). Smaller amounts were generally recorded in larvae from Red Lodge than in larvae from the other streams. In 1959 quantities in larvae from Stoughton far exceeded those in larvae from the other streams, probably as a result of the washing into Stoughton stream of large quantities of mud and sand from drains that were being dug further upstream.

## DISCUSSION

Ivanova (1958) found that *Chloëon dipterum* ingested several dead animals including fish fry, dragonfly larvae, and small oligochaetes, and also fed upon the fungus *Saprolegnia*. In the present study fragments of arthropod cuticle occurred very rarely in the food under natural conditions although larvae were observed to ingest dead *Daphnia* in the laboratory. However, larvae made no attempt to capture live crustacea in the manner described by Wissmeyer (1926) whose observation has not been verified by subsequent work and must be regarded as doubtful. No fragments of arthropod cuticle were found in the gut contents of *Baëtis rhodani* collected in the field. *Baëtis* sp. did not ingest dead animals in the experiments performed by Ivanova, or tissue of *Elodea canadensis* or *Ceratophyllum demersum* both of which were ingested freely by *Chloëon dipterum*. It is evident that *C. dipterum* is capable of ingesting a more varied diet than *Baëtis rhodani* under certain conditions, but there are no obvious structural differences in the mouthparts of the two species that would account for this. Further experimental work on the extent and nature of food selection by bottom-feeding invertebrates will be of great interest in this respect.

In the natural habitat both species of larvae subsisted mainly on a mixed diet of detritus, mineral particles, vascular plant tissue and algae. Of these components detritus formed by far the greatest proportion of the total volume of the food ingested in both species; vascular plant tissue was often absent, and filamentous algae were often present in very small amounts particularly in *B. rhodani*.

In view of its high cellulose content Jones (1950) considered that detritus was of low nutritive value and that animals feeding upon it had a large alimentary canal and fed continuously. Van Heyningen (1954) found that detritus had a very low nutritive value for *Daphnia* and *Simocephalus*. Moon (1938) suggested that a large quantity of algae in the food was necessary for growth to take place in *Caenis* and *Leptophlebia*, and Teal (1957) showed that when larvae of *Anatopynia dyeri* (Chironomidae) fed upon detritus in the absence of plant and animal food their average weight decreased. On the other hand Gatjen (1926) considered that detritus was utilized as an important food component in *Phryganea* (Trichoptera). It is probable that the nutritive value of detritus varies locally and seasonally according to its composition. For example at Quenby Willows pond the detritus was largely composed of the faecal pellets of *Asellus meridianus*, and this material was probably of relatively high nutritive value as Levanidov (1949) showed that *A. aquaticus* assimilated not more than 70% of the calorific value of leaf material ingested. On the other hand in streams, and ponds receiving streams, the detritus for much of the year is probably composed mainly of inorganic particles and vegetable matter decomposed to the extent of crude fibre that according to Birch & Clark (1953) is indigestible. It is possible that those mayfly larvae that subsist upon such a complex mixture of materials have a different complement of enzymes to those that subsist upon a homogeneous diet of algae. The rate of defecation of *Chloëon dipterum* and *Baëtis rhodani* feeding upon detritus in the laboratory was rapid, the usual time for passage of food through the gut being approximately half an hour. This agreed with Jones's suggestion that rapid continuous feeding is characteristic of detritus-feeding animals, and suggested that only a small proportion of the calorific value of this food material was utilized. Larvae of *Chloëon dipterum* which were observed feeding upon filamentous algae and higher plant tissue appeared to expend a greater amount of energy ingesting these food materials by slow chewing movements of the mouthparts than in rapidly brushing up fine detritus (Brown 1961). In the case of the former food materials the rate of defecation was relatively slow in correlation with the rate of mouthpart action. Algae were thus retained for longer in the gut than was detritus, and in view of the thorough digestion of many species (Brown 1960) it is probable that a far higher proportion of the calorific value of this food material is utilized. However, when feeding under natural conditions, the larvae of *C. dipterum* and *Baëtis rhodani* ingest mainly detritus, the food material that requires the least expenditure of energy for its collection.

Besides the qualitative differences in the composition of the food of the two species described previously, larvae of *B. rhodani* usually contained more food than larvae of *Chloëon dipterum* of the same size. This was particularly marked in the winter when larvae of *C. dipterum* appeared translucent while a dark mass of food was obvious in *Baëtis rhodani.* A greater food intake is to be expected in *Baëtis* in correlation with the greater amount of energy it expends in maintaining itself in the flowing water of a stream and in collecting food in this habitat. Fox & Simmonds (1933) showed that the basal rate of metabolism of *B. rhodani* was three to four times as great as that of *Chloëon dipterum* between the temperatures of 10 and 16° C, and the results of the present work (compare the May-July values in Tables 1 and 4) show that the consumption of detritus by *Baëtis rhodani* over this temperature range was approximately three to four times greater than that of *Chloëon dipterum,* a fact which indicates that the efficiency of food absorption is similar in the two species. In the winter the consumption of detritus by *Baëtis* exceeded that by *Chloëon* by a far greater amount, and this was probably due to the relatively greater reduction in the activity of *C. dipterum* at low temperatures (see below).

Physical factors operate in two ways to produce seasonal differences in the composition of the food of animals: by affecting the intensity of their activity and by altering the composition and quantity of the food available to them. It is difficult to assess the relative importance of these two effects in mayfly larvae because of the difficulty in measuring changes in the amount of a material like detritus in the habitat, and the lack of information on the effect of low temperatures on the activity of the larvae. Low temperature appeared to exert a greater direct influence on the amount of food ingested by *C. dipterum* than *Baëtis rhodani,* a result that provides a consequence in the natural habitat of the difference in thermal indices between the two species demonstrated by Whitney (1939). This author found that *Chloëon dipterum* tolerated higher temperatures (28-30° C) than *Baëtis rhodani* (21°) and the results of food analyses show that these species also have different tolerances at the other end of the temperature scale. *B. rhodani* is able to maintain a high rate of ingestion and growth at temperatures at which *Chloëon dipterum* practically ceases to feed. It is impossible to measure the growth-rate of *Baëtis rhodani* accurately by measuring the mean size of successive samples of larvae, because the rate of addition of small larvae to the population due to the delayed hatching of eggs is unknown, but it is probable that growth continues throughout the winter whereas in *Chloëon dipterum* it ceases from November to March. The available information on the life cycles of the two species in England suggest that *C. dipterum* is univoltine (Brown, unpublished data) whereas *Baëtis rhodani* completes two main generations each year (Macan 1957). This difference in life cycles must depend to a great extent on the relatively greater metabolic activity of *B. rhodani* at low temperatures.

Although the amount of food ingested by *Chloëon dipterum* appeared to be directly related to temperature during winter, spring and early summer, there were occasions towards the end of the summer when there was an abrupt decline in the amount of food ingested, even though temperatures remained the same or rose higher. No fluctuation in the amount of food was observed in the habitats which could account for this, and temperatures were not high enough to exert a directly depressive effect on the activity of the larvae (a maximum of 21° C was recorded at Whites Barn in comparison to the thermal index of 28-30° recorded by Whitney for *C. dipterum*). Fox & Wingfield (1937) showed that *C. dipterum* was physiologically adapted to the pond habitat in being able to absorb oxygen at a rate that was independent of the concentration of oxygen in the surrounding water down to concentrations of 1·4 ml/l. Both they and Wingfield (1939), however, remark that the oxygen concentration often falls as low as 1·5 ml/l. in ponds, and it seems likely that under certain conditions low oxygen concentration would produce a reduction in the activity of *C. dipterum* and thereby a reduction in the amount of food ingested. Prokesova (1959), studying small ponds, found that stratification of the water into oxygen and hydrogen-sulphide layers existed, and that on several occasions in late summer oxygen was not present in measurable amounts. The strong smell of hydrogen sulphide at Baggrave indicated that oxygen conditions were very poor, and it is probable that at this time of the year the food intake of *C. dipterum* in all the habitats was lowered to some extent by the effect of low oxygen concentration in the water. This could either have affected the larvae directly, or indirectly by their being driven away from the richest source of food, the detritus of the bottom and that coating the bottom plants, by the rising stratum of water containing hydrogen sulphide and lacking oxygen. It is to be expected that this effect would be manifest in isolated or short series of samples, and not synchronous in all the habitats, because of the rapid changes and local differences that occur in the physical conditions in small ponds.

Algae were an unimportant food component in *C. dipterum* and *Baëtis rhodani* on the basis of the proportion of the total volume of the gut contents that they occupied. This finding conflicts with the results obtained by several authors for these and related species (see p. 55) who stress the importance of algae as the main food component. While it is probable that detritus has been ignored by some workers as a food component when in fact it was present, it is likely that local variation if feeding is responsible to some extent for this disagreement. The most important factor producing such variation is probably local variation in the food available to the larvae but it is also possible that local races of some species exist of which the larvae differ in their feeding habits.

Local differences were found in the composition of the food of *Chloëon dipterum* and *Baëtis rhodani* which were generally correlated with the nature and abundance of the food available in the habitats. Similar local differences were recorded by Hynes (1941) in the diet of *Isoperla grammatica* (Plecoptera), which was more carnivorous in character in small streams than in rivers. Hynes suggested that this was due to the smaller amount of algae and the larger numbers of animals present in small streams, and demonstrated that in such a habitat the larvae grew more rapidly and reached a larger size than in rivers. The implication contained in these results, that the nutritive value of the diet of *Chloroperla* was directly related to its animal content, was not verified experimentally. It was observed in samples collected on the same day that there were differences between the local populations of both *Chloëon dipterum* and *Baëtis rhodani* in the maximum and mean size of the larvae, and it was considered possible that the local size differences were related to local differences in the proportion of algae in the diet. In order to investigate this measurements were made of the mean lengths of large numbers of samples of larvae collected near the places from which the samples for the analysis of the gut contents were collected. Evidence that local size differences did exist but were not correlated with diet was found in the case of the populations of *B. rhodani* at Fludes Lane and Stoughton. Throughout 1957 the mean length of Fludes Lane larvae was greater than that of Stoughton larvae collected at the same time. This difference between the populations was obvious to the naked eye and was not due to a different rate of hatching of eggs because the maximum length of larvae from Fludes Lane was consistently greater than that of larvae from Stoughton. Over this period several analyses of the gut contents were made and showed that the diet of Fludes Lane larvae contained more algae than that of Stoughton larvae. That the size differences were not correlated with this difference in the composition of the diet was shown by the fact that, as a result of a decrease in the maximum length of larvae from Fludes Lane of about 3 mm, the size differences between the populations disappeared while the composition of the diet remained the same. It is unlikely that this was due to the effect of collecting samples because larvae were returned to the same place alive after measuring. A number of reasons other than local differences in the diet may be suggested to account for local differences in the size of *B. rhodani*. Harker (1953a) found that the distribution of this species in a stream was not random and that small larvae tended to congregate at the edges, and Macan (1957) found that larvae migrated downstream when large. In view of these facts it is unwise to attempt to relate local differences in size with diet in the cases of *B. rhodani* and *Chloëon dipterum* and probably many other aquatic larvae.

In addition to the effect of local differences in available food, variation in the composition of the gut contents between intraspecific populations of ephemeropteran larvae may be due to the selection of different foodstuffs by local races. In the Ephemeroptera such races have been shown to exist differing in activity rhythms (*Ecdyonurus*, Harker 1953b), size (*Baëtis baddamsae* Harker, Harker 1950), and thermal resistance (*Rhithrogena semicolorata*, Whitney 1939). In other aquatic organisms there are similar examples for size and oxygen consumption (Hynes 1954, Fox & Simmonds 1933 and Washbourn 1936). In the absence of any evidence to the contrary the existence of local races differing in feeding habits must be considered as a possible factor producing local differences in the food ingested by ephemeropteran larvae.

It is probable that the relatively large quantities of mineral particles ingested by *Baëtis rhodani* are not entirely without nutritive value. Wilson (1955) has demonstrated the importance of the film of micro-organisms present upon sand particles in the settlement of *Ophelia bicornis*. Such a film of micro-organisms is probably also present upon particles in fresh water and may provide an important source of food for small larvae.

## ACKNOWLEDGMENTS

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## SUMMARY

1. The foregut contents of *Chloëon dipterum* (L.) and *Baëtis rhodani* (Pictet) collected from ponds and streams in south-east Leicestershire at approximately fortnightly intervals over a period of 18 months were analysed.

2. The food of both species consisted mainly of detritus. That of *Chloëon dipterum* contained a larger proportion of filamentous algae and a smaller proportion of mineral

particles than that of *Baëtis rhodani*; the total amount of food present in the gut in winter and early spring was far less than in *B. rhodani.*

3. Seasonal and local differences occurred in the total amount of food present in the gut and in the proportion of detritus relative to the other food components which were algae, vascular plant tissue and mineral particles. The food of very small larvae of both species consisted mainly of detritus with a few unicellular algae.

4. The factors responsible for the seasonal fluctuation in the quantity and composition of the food ingested are discussed. In *Chloëon dipterum* temperature appeared to be the dominant factor, whereas in *Baëtis rhodani* this was the variation in the food available in the habitat.

5. Differences in the food ingested by different populations of *Chloëon dipterum* and *Baëtis rhodani* reflected differences in the food available in the habitats. In the case of *B. rhodani* such differences were shown not to be correlated with size differences between the populations.

6. Differences in the diet according to the size of the larvae were found in both species.

7. The significance of the relatively small quantities of algae found in the food is discussed.

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